TITLE PAGE

Title:

Bargaining in chimpanzees (*Pan troglodytes*): the effect of cost, amount of gift, reciprocity and communication

Running title:

Dictator and Ultimatum games in chimpanzees

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AUTHOR FOOTNOTES:

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Contributions

Conceived and designed the experiments: NBG, JC, AD, MC. Performed the experiments: NBG, AD. Analyzed the data: CV, JC, NBG. Interpretation of data and writing of the paper: JC, NBG, CV.

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ABSTRACT:

Humans routinely incur costs when allocating resources and reject distributions judged to be below/over an expected threshold. The Dictator/Ultimatum Games (DG/UG) are two-player games that quantify prosociality and inequity aversion by measuring allocated distributions and rejection thresholds. Although the UG has been administered to chimpanzees and bonobos, no study has used both games to pinpoint their motivational substrate. We administered a DG/UG using pre-assigned distributions to four chimpanzee dyads controlling for factors that could explain why proposers' behavior varied substantially across previous studies: game order, cost for proposers and amount for recipients. Moreover, players exchanged their roles (proposer/recipient) to test reciprocity. Our results show that proposers offered more in the DG than in the non-social baseline, particularly when they incurred no cost. In UG, recipients accepted all above-zero offers, suggesting absence of inequity aversion. Proposers preferentially chose options that gave larger amounts to the partner. However, they also decreased their offers across sessions, probably being inclined to punish their partner's rejections. Therefore, chimpanzees were not strategically motivated towards offering more generously to achieve ulterior acceptance from their partner. We found no evidence of reciprocity. We conclude that chimpanzees are generous rational maximizers that may not engage in strategic behavior.

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INTRODUCTION

The last decade has produced abundant comparative research with non-human primates on the evolutionary origins of human prosociality and the sense of fairness. Even though great apes such as chimpanzees engage in cooperative hunting and food sharing in the wild, laboratory studies have consistently found that chimpanzees do not usually provide windfall resources to partners at no cost (Silk et al., 2005) and do not understand justice as humans do (eg. Riedl, Jensen, Call, & Tomasello, 2012). Generally, testing procedures involve two conspecifics facing a food distribution task that may potentially trigger phenomena such as inequity aversion (eg. Brosnan & de Waal, 2003; but see Engelmann, Clift, Herrmann, & Tomasello, 2017), no cost prosociality (eg. Horner, Carter, Suchak, & de Waal, 2011), food sharing (Silk, Brosnan, Henrich, Lambeth, & Shapiro, 2013) or reciprocity (eg. Amici et al., 2014). Bargaining games, such as the dictator (DG) and the ultimatum (UG) games (Güth, Schmittberger, & Schwarze, 1982) are particularly appealing because they combine each of these phenomena simultaneously.

In both games, a proposer splits a windfall in any way she desires with her partner. Whereas the DG recipient is passive and has to accept the proposer's offer, the UG recipient can either accept or reject the offer. If the offer is accepted, each partner receives the corresponding split but if the offer is rejected nobody receives anything. Since the DG recipient cannot affect the final outcome of the distribution, any non-zero offer by the proposer indicates the latter's prosocial tendency. In contrast, the proposer's offer in the UG is composed of her prosocial tendency plus her strategic estimation of what the recipients are likely to accept. When confronted with resource distribution games, humans take into account their own and their partners' prosocial tendencies and social aversions to avoid conflict. Although there are substantial cross-cultural differences (Camerer, 2003; Engel, 2011; Güth & Kocher, 2014; Henrich et al., 2005; Henrich, Heine, & Norenzayan, 2010), human proposers make offers above zero in both games, usually higher in the UG than the DG, and human recipients often reject options smaller than 20% and sometimes even bigger than 50%. Taken together, these results contradict the rational maximizer's perspective since some humans are willing to give and reject at their own cost (Güth & Kocher, 2014). Importantly, we use the term "rational maximizer" to indicate that when there is something to be gained, subjects take it regardless of what someone else got as a result, even if that someone was responsible for creating that choice in the first place.

Current interest in the evolutionary roots of fairness and its psychological underpinnings have led researchers to confront pairs of individuals with various social dilemmas including several versions of the UG (Jensen, Call, & Tomasello, 2007; Kaiser et al., 2012; Proctor, Williamson, de Waal, & Brosnan, 2013). Following the mini-ultimatum procedure developed by Falk and colleagues (2003), Jensen et al. (2007) presented dyads of chimpanzees with preselected pairs of quantities (e.g., 5/5 vs. 8/2, with the first of each pair representing the proposer's allocation). The proposer could select one of the pairs by pulling a rod that brought the offer halfway. Then, the recipient accepted by pulling another rod that delivered the offer to both subjects or rejected by not pulling during 60s, thus ending the trial without any food within reach. Kaiser and colleagues (2012) tested chimpanzees and bonobos in a procedure where they allowed the proposers to "steal" some of the food originally allocated to the recipient before making an offer, to see whether this enhanced rejections. In both studies, proposers did not incur cost to make equal offers whereas recipients showed no inequity aversion since they never rejected non-zero outcomes. Consequently, unlike humans, chimpanzees and bonobos behaved as rational maximizers. With regard to recipients, one argument against this conclusion was that 0-options were accepted approximately half of the time (Jensen et al., 2007). According to some authors, chimpanzees might not have behaved as rational maximizers (Brosnan, 2013). According to others (Henrich & Silk, 2013), rejecting 0-option half of the time implies responding at chance, which is compatible with rational maximizing as both accepting and rejecting leads to zero outcome. Smith and Silberberg (2010) offered an alternative explanation. They found that apes' data were reproducible in humans by increasing the delay to reject from 1 to 5 minutes. Namely, when humans were forced to wait 5 minutes (instead of 1) to reject an offer, they tended to accept anything to initiate the next trial and thus increased their likelihood of obtaining something. This means that 60s may have been too long to wait for chimpanzees (Jensen et al., 2007) who may have accepted 0-offers to initiate a new trial with better prospects.

Another relevant aspect for bargaining methodologies is the way proposers make offers and recipients respond to them. One solution is using token exchange procedures to substitute the direct presence of food for an object (the token equals some distribution of food) and to emulate a physical interchange. Proctor and colleagues (2013) compared chimpanzees' responses in an UG and in a preference test using tokens, each of them allocating a different amount of food to the proposer and the recipient (5/1 vs. 3/3). Proposers selected one token, gave it to the recipient who could then either give it to a begging experimenter (accept) or keep it during the next 30s (reject). In their preference test, proposers gave tokens directly to the experimenter while a naïve passive recipient sat in the adjacent cage. Although the authors treated this preference test as a DG, this is unwarranted because the proposer did not give anything directly to the recipient, turning it into a non-social game (Henrich & Silk, 2013). The authors found that proposers selected the 3/3 token more often in the UG than in the preference test. However, the interpretation of this result is controversial. Henrich and Silk (2013) pointed out that the change towards 3/3 was not different from chance in two out of the three dyads. In response, Brosnan and de Waal (2014) claimed that this change of behavior between conditions reflected second-order inequity aversion as chimpanzees might have anticipated a conflict. However, since rejections never occurred and no experimental evidence for that potential anticipation was provided, this remains a mere conjecture. Pairing a prototypical DG with an UG would have been highly desirable because it would have allowed researchers to distinguish intrinsic (i.e., give) from strategic (i.e., give to receive) prosociality. Furthermore, the absence of 0-options or the inclusion of a begging human experimenter may have substantially hindered the appearance of rejections.

In sum, the evolutionary picture of fairness based on the UG remains rather ambiguous. Whereas two studies characterize ape proposers as selfish (Jensen et al., 2007; Kaiser et al., 2012) another study characterizes them as prosocial (Proctor et al., 2013) but in any case, whether this is based on intrinsic or strategic motivation remains unclear. Moreover, although all studies have shown that recipients accept any offers above zero, there are different interpretations about the absence of rejections in recipients (Jensen, Call, & Tomasello, 2013; Proctor, Williamson, de Waal, & Brosnan, 2013). The goal of this study is to shed light on these issues by comparing chimpanzees' responses in an iterated DG/UG that manipulated the cost to the proposers and the size of the gift to recipients. Players faced each other across a table and the proposer selected one of two food windfalls by pulling a rope that distributed it among the two players. Moreover, in the UG the recipient could accept the proposer's choice by pulling another rope or reject it by not pulling for 15s (see Figure 1b). We are aware that a go/no go paradigm for rejections in UG diminishes exact comparison with UG human procedures, but the reduction of rejection time to 15s decreases the likelihood of unmotivated refusals (Smith & Silberberg, 2010). Two key features of our study deserve special mention. First, our ABACA design alternated between non-social (A) and social games (B and C represented DG or UG), a feature that allowed us to obtain a reliable estimate of the baseline tendency to select each option in the absence of a partner as well as their understanding of the game and the stability of their response.

Second, we manipulated the cost for proposers and the size of the gift for the recipient. The latter allowed us to know whether proposers considered their partner's payoff in their offers and whether recipients rejected based on advantageous (rejection of high gift) or disadvantageous (rejection of low gift) inequity aversion. The inclusion of a 6/0 option measured the likelihood of rejecting when receiving nothing and served as an anchor point against which all other options were pitted (6/3, 5/3, 5/9, 6/9, see Table 1 for further information). Importantly, we are aware that using small quantities may produce different recipients' responses than larger rewards. However, it is not only the design feasibility that justifies their use, but also the idea that only when differential rates between the rewards are small, moral emotions are activated, thus allowing us to explore whether they are present in non-human animals. Finally, chimpanzees played reciprocal trials (i.e. every dyad played the same condition switching roles) to see whether second-order inequity aversion or reciprocity occurred. We also scored any communicative acts (see SI).

Figure 1 around here

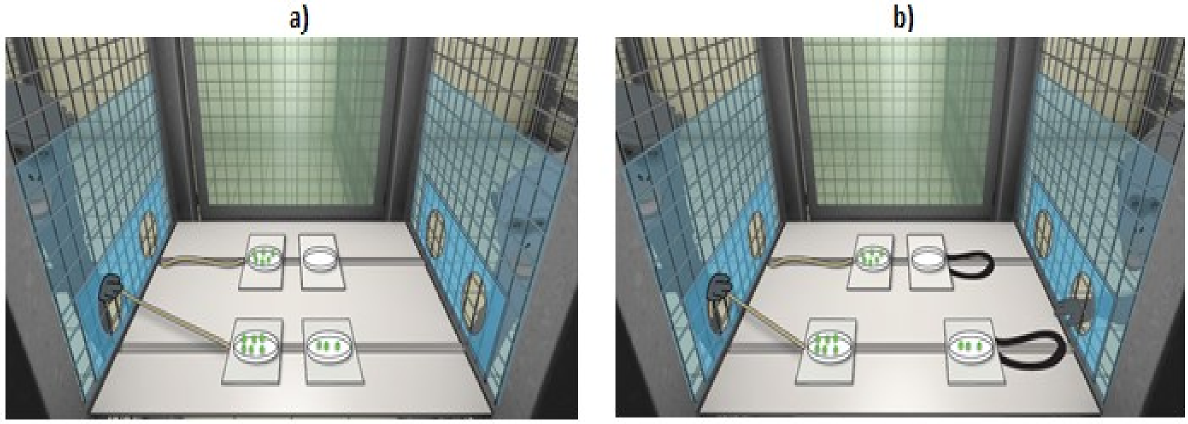

Figure 1. Illustration of the apparatus for the DG (a) and UG (b) in the condition 6/0 (background) 6/3 (foreground). The proposer is depicted on the left and the recipient on the right. In the DG, the recipient cannot reject the offer. In the UG, the recipient can respond to the offer by pulling the U-shaped rope (accept) or not (reject) once the proposer has chosen one option.

METHODS

The Committee of Bioethics at the University of Barcelona (IRB00003099) and the ethics committee of the Wolfgang Köhler Primate Research Center (WKPRC) approved the study.

Participants. Six chimpanzees (4 males; mean age= 15 years) housed at the WKPRC in Leipzig Zoo (Germany) participated in the study. We tested four dyads. Even though dyads consisted of forced partner combinations, we carefully chose kin or nonkin social tolerant partners because previous studies had shown those partners to be successful in cooperation (eg. Melis, 2006; Suchak, Eppley, Campbell, & de Waal, 2014). Two subjects (Lobo, Kofi) played twice to informally explore whether they changed their behavior depending on the partner they were playing with (see Table S1 for detailed information upon age, sex, rearing history and previous participation in Jensen et al.'s study (Jensen et al., 2007)).

Materials. We used two similar apparatuses for the UG and DG (see Figure 1). The DG apparatus consisted of a PVC table with two parallel guide rails running from the proposer's side to the recipient's side. A pair of trays located on top of each rail holding various food distributions constituted one of the options that the proposer could select by pulling a rope so that the trays on the corresponding rail moved in opposite directions: the closest tray moved toward the proposer and the farthest tray toward the partner. The UG apparatus was similar except that when the proposer pulled, the trays in that rail moved in opposite directions but stopped halfway to the recipient making a piece of Velcro accessible to him so that he could decide whether to pull to complete the movement of the trays (accept) or not (after 15s reject, see Video for illustrative examples of acceptance and rejection and SI for further detailed information about the apparatus).

Table 1 around here

Table 1. Conditions and maximizing choices. Quantities used in non-social (Door Open/Door Closed) and social games. Depicted are the outcomes in each non-social condition based on a maximizing outcome. We also provide the labels of each pair of options used in social games to illustrate the factors assessed (cost for the proposer; gift for the recipient)

Non-social Door Open	Choice if maximization	**Non-social Door Closed**	Choice if maximization	**Social games UG/DG**	Labels in Social games	
					Proposer	Recipient
6/0 and 6/3	6/3	6/0 and 6/3	chance	6/0 and 6/3	No Cost	Small gift
6/0 and 5/3	5/3	6/0 and 5/3	6/0	6/0 and 5/3	Cost	Small gift
6/0 and 5/9	5/9	6/0 and 6/9	chance	6/0 and 6/9	No Cost	Large gift
0/0 and 0/3	0/3	6/0 and 5/0	6/0	6/0 and 5/9	Cost	Large gift

Food and conditions. We used small pieces of grapes/pellets, depending on dyads' food preferences. We configured the conditions following Hanus and Call (2007) to have higher differences and lower ratios between final outcomes. Thus, we had four conditions with a default 6/0 option pitted against another option controlling for cost to be generous (in no cost conditions, the proposers could be generous with their partners for free by always earning 6 pieces of food whereas in cost conditions that would imply losing 1 piece of food by deciding between 6/0 and 5/x) and size of gift (in small gift conditions, the proposers could raise their partner's outcome to 3 pieces of food, less than their own profit (i.e. 6/0 and 6/3), whereas in large gift conditions, the partner's outcome would surpass their own (i.e., 6/0 and 6/9). We varied some pairs of quantities between non-social and social games (see Table 1) to test for the chimpanzees' understanding of the task. The condition 0/0 and 0/3 increased the salience of the recipient's side allowing us to analyze whether subjects payed attention to the consequences of their choices with respect to the pay-offs on their side. The condition 6/0 and 5/0 allowed us to ensure that subjects discriminated quantities (6 vs 5) and the cost was significant to them.

Procedure and design. We used an ABACA design (A: training non-social, B/C: social games). The training consisted of 6 conditions that were played across 8 sessions of 12 trials each. We conducted the training before the social games and post-training after each social game, therefore each subject played 24 non-social sessions. The state of the door was relevant during the training. The closed door did not allow the subject to gain access to the adjacent cage. Therefore, maximizing the pay-off only required paying attention to the options on the subject's side (the food allocated to the other side could not be obtained). Thus, we could control whether subjects would preferentially choose maximizing quantities (eg. 6/0, obtaining 6, rather than 5/3, obtaining 5, see Door close conditions in Table 1). The open door allowed subjects access to the adjacent cage. Therefore, maximizing the pay-off required the subject to pay attention to trays on its side as well as on the other side, understand how trays moved and avoid natural impulses to pick always the closest and highest quantities in order to choose the maximizing option (eg. 5/3, obtaining 8, rather than 6/0, obtaining 6, see open door conditions in Table 1). Table 1 shows how subjects should vary their choices depending on the state of the door to prove their understanding of the game. In each session, one given condition was played during three non-consecutive trials. Chimpanzees played alone and passed the training when they chose the maximizing option at least in 80% of the trials per condition. We counterbalanced the order of the conditions, the sides of each option and the room where the actor played.

Each dyad played both UG and DG. Each game consisted of 8 sessions, 12 trials per session. The proposer and recipient roles alternated from trial to trial (e.g., in trial 1 the condition 6/0 and 6/3 is played; Alex plays as proposer and Jahaga as recipient; in trial 2, the condition is maintained but Alex is the recipient and Jahaga the proposer). Therefore, to analyze reciprocity we measured whether dyads matched their choices in each pair of reciprocal trials and whether this remained constant across sessions. The order of the games was counterbalanced across dyads (i.e., ABACA or ACABA). Every trial started with the experimenter placing the food out of sight from the participants. When the proposer chimpanzee chose one option, in DG, both players got access to the food immediately (see Figure 1a) whereas in UG, the experimenter waited for 15 seconds for the recipient to pull from the Velcro (see Figure 1b). If the recipient did not pull, the food was removed. Regardless of rejection or acceptance, the inter-trial interval remained constant.

ANALYSIS

We used Generalized Linear Mixed Models (GLMM; (Baayen, 2008)) with binomial error structure and logit link function to analyze subjects' choices (see Table 2 for an overview of the fitted models). When subjects delivered food to the opposite side we scored 1, otherwise we scored 0. We also examined when recipients in the UG rejected offers and whether the offer in the previous trial (or the average offer in the previous session) affected the offer of the prior recipient in the current trial (short-term reciprocity). We examined the effect of communicative attempts between proposers and recipients. We coded two behaviors: "pointing", if the subjects placed their index finger or their hand through the decision window for more than 3s and "interaction", when the subjects touched or passed objects to each other through the mesh. We analyzed the two different responses separately. To examine whether they performed any of these responses at different rates in each social game we used the frequency of these responses as dependent variables. Moreover, as pointing and interaction could enhance the probability of the proposer to deliver more food (i.e. choosing 6/3 instead of 6/0) or to incur a cost (i.e. choosing 5/3 instead of 6/0), we analyzed whether these communication attempts were related to the proposer's choice. For further information on the model specification, random effect structure, model stability and assumptions, see SI.

Table 2 around here

Table 2. Summary of the main GLMMs performed. See more information in SI.

GLMM	Data analyzed	Dependent variables	Predictor variables
Game understanding (GLMM01)	non-social door open and door closed, common conditions	Food for recipient's side	cost, gift, state of door, session, trial number, training phase, cost x door
Difference UG/DG (GLMM02)	UG, DG, all conditions	Food for recipient	game, cost, gift, (all 2-way interactions), session, trial number
Change of behavior between social and non-social games (GLMM03)	non-social (door closed), UG, DG, common conditions	Food for recipient's side	game, cost, game x cost
Rejection (GLMM04)	UG, all conditions	Rejection of offer	cost, gift, session, trial number, cost x gift
Reciprocity (GLMM05 / GLMM06)	UG, DG, all conditions	Food for recipient's side	game, cost, gift, previous prosocial offer, trial number, session, and all 2-way interactions between previous prosocial offer and game, cost, and gift
Pointing (GLMM07)	UG, DG, all conditions	Pointing	game, session, trial number
Effect of pointing on prosocial choices (GLMM08)	UG, DG, all conditions	Food for recipient	recipient pointing, game, cost, session, trial number, type x game, type x cost

RESULTS

Non-social games (training)

Figure 2 presents the proportion of trials in which chimpanzees playing alone selected the option that delivered food to the opposite side instead of the default 6/0 as a function of cost at the subject's side and door state. GLMM01 was significant compared to the null model (likelihood ratio test: χ^2=105.58, df=6, p<0.001). We only found a significant interaction between door and cost (estimate ± SE: -1.00 ± 0.29, χ^2=11.77, df=1, p<0.001; see Table S4). Post-hoc tests revealed that chimpanzees maximized their payoffs in cost condition when the door was open and they could gain access to 5+3 pieces of food than when it was closed and they would only get 5 pieces (1.35 ± 0.21, χ^2=44.69, df=1, p<0.001). In the no cost condition, subjects' choices were not significantly affected by the door state (0.35 ± 0.21, χ^2=2.87, df=1, p=0.090). Moreover, subjects preferentially selected 6/0 over 5/0 (80.1%, T^+=21, N=6, p=0.031) when the door was closed and 0/3 over 0/0 (97.2 %, T^+=21, N=6, p=0.031) when it was open (see SI for additional analyses). Taken together these results provide evidence that subjects paid attention to the quantities on their side and on their partner's side. Furthermore, they adjusted their choices to the state of the door to maximize their outcome.

Figure 2 around here

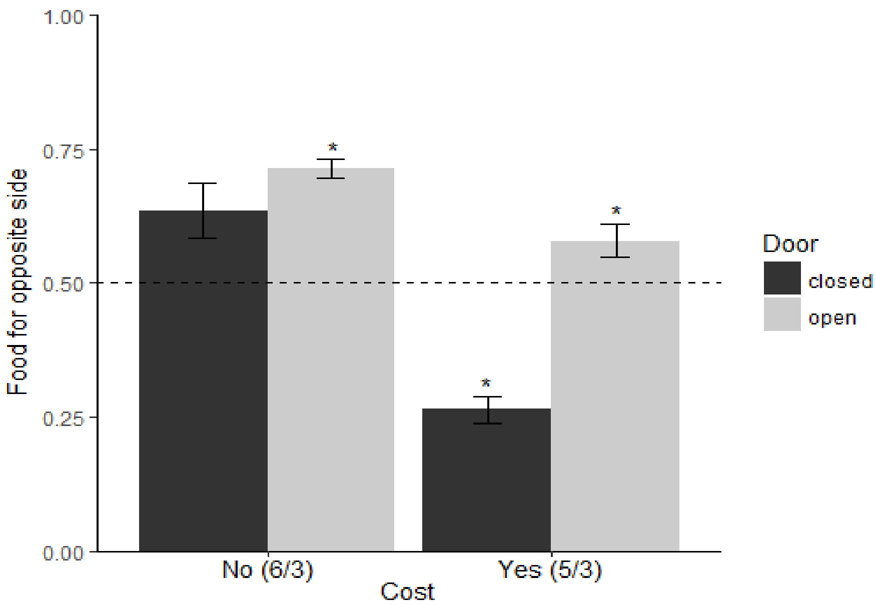

Figure 2. Proportion of trials (mean ± SE) of the common conditions in the Door open/closed non-social tests in which chimpanzees preferred the option that delivered food to the opposite side (over the default 6/0 option) as a function of cost and door state. * denotes significant deviations from the hypothetical chance level (dashed line), p<0.05, Wilcoxon signed-rank tests.

Social games

Figure 3 presents the proportion of trials in which chimpanzees selected the options that delivered food to their partner's side (compared to the default 6/0 option) as a function of game, cost and gift. GLMM02 (see SI) was significant compared to the null model (χ^2=82.01, df=8, p<0.001), however we found no significant interactions (all p>0.1).

Figure 3 around here

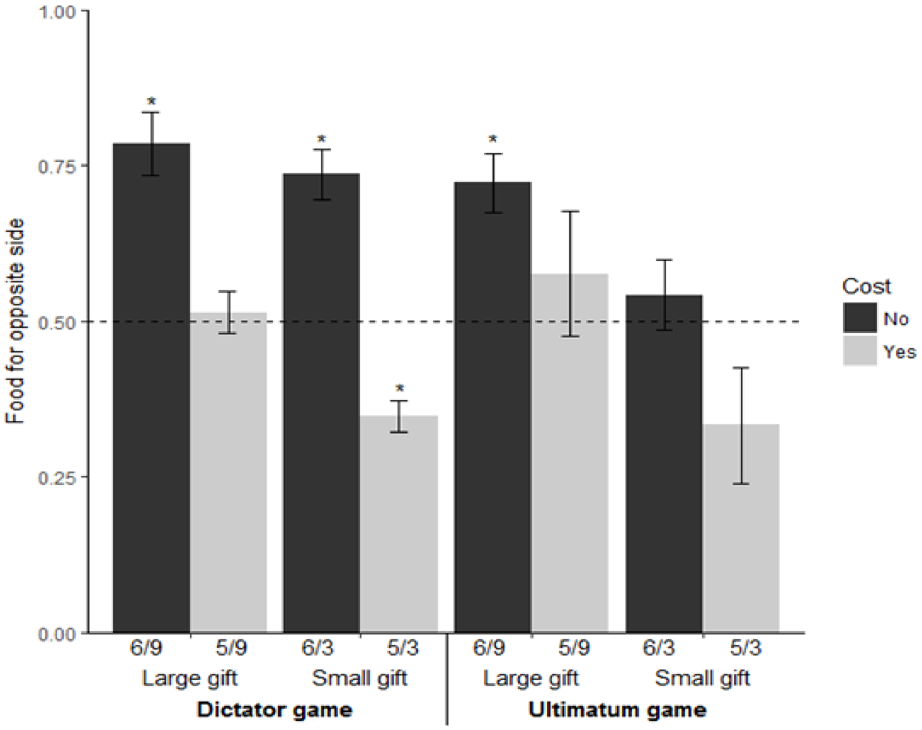

Figure 3. Proportion of trials (mean ± SE) in which chimpanzees preferred the option that delivered food to their partner's side over the default 6/0 option as a function of game (DG, UG), size of the gift for the partner (x/9 vs. x/3), and cost at the subject's side (cost: 5/x; no cost: 6/x). * denotes significant deviations from the hypothetical chance level (dashed line), p<0.05, Wilcoxon signed-rank tests.

A reduced model without the 2-way interactions was significant compared to the null model (χ^2=76.93, df=5, p<0.001; see Table S5). Subjects were more willing to deliver food to the partner when there was no cost (-1.11 ± 0.16, χ^2=52.96, df=1, p<0.001) and when the gift for the partner was large (-0.63 ± 0.16, χ^2=16.91, df=1, p<0.001). Moreover, the likelihood to deliver food to the partner decreased over sessions (-0.18 ± 0.08, χ^2=5.66, df=1, p=0.017). There was no significant difference between the games (-0.24 ± 0.15, χ^2=2.37, df=1, p=0.124) or a significant main effect of trial number (-0.007 ± 0.08, χ^2=0.008, df=1, p=0.930). Taken together these results show that chimpanzees played DG and UG in a similar way. They delivered food to their partners predominantly when this did not entail a cost for them but they were also more generous with larger amounts of food for the partner.

Figure 4 presents the proportion of trials in which chimpanzees selected the option that delivered food to their partner's side as a function of game and proposer's cost. We compared the social games and the non-social training (door-closed condition; data pooled across the training phases because our analyses had shown that performance remained unchanged throughout training phases, see SI). GLMM03 was significant compared to the null model (χ^2= 98.56, df=3, p<0.001; see Table S6). Proposers were more willing to deliver food to the other side when there was no cost for them (-1.40 ± 0.15, χ^2= 92.63, df=1, p<0.001). We found a significant effect of game (χ^2= 6.72, df=2, p=0.035), specifically, subjects delivered more food to the other side in DG compared to the non-social training (0.43 ± 0.19, z= 2.33, p=0.020) but not between the UG and training (-0.06 ± 0.19, z= -0.34, p=0.736). Consequently, chimpanzees only chose the prosocial options significantly more often when there was no cost associated with it in the DG compared to when they played alone.

Figure 4 around here

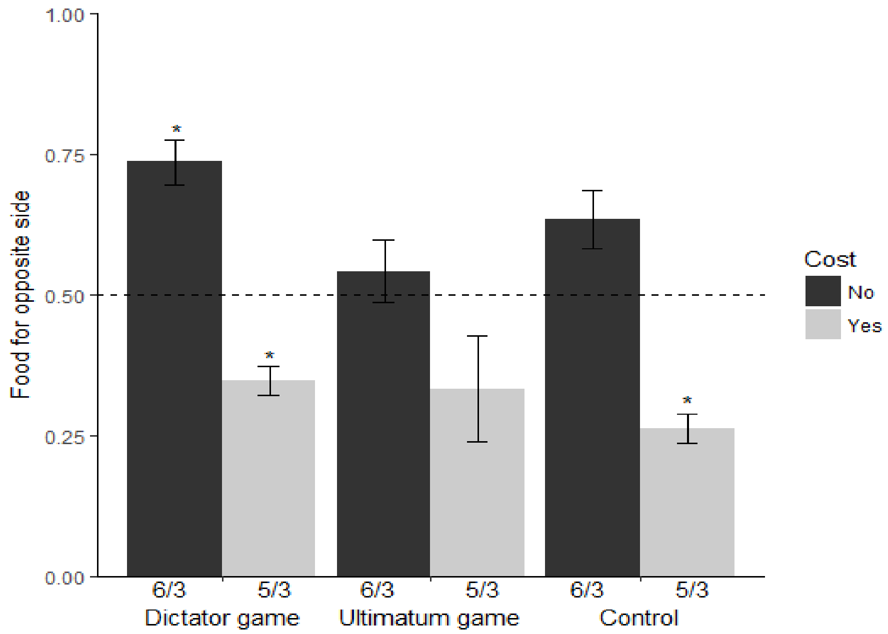

Figure 4. Proportion of trials (mean ± SE) in which proposers selected the option that delivered food to their partner's side as a function of game (non-social control, DG, UG) and cost for the proposer. *denotes significant deviations from the hypothetical chance level (dashed line), p<0.05, Wilcoxon signed-rank tests.

We also analyzed the two games separately. In both the UG and DG, proposers were significantly more willing to deliver food to the partner when they incurred no cost (UG: -0.91 ± 0.22, χ^2=17.69, df=1, p<0.001; DG: -1.33 ± 0.28, χ^2=8.27, df=1, p=0.004). In the UG, this happened also when the gift for the partner was large (0.88 ± 0.22, χ^2=16.52, df=1, p<0.001). In contrast, no significant effect of gift was found in DG (0.39 ± 0.22, χ^2=3.16, df=1, p=0.076). Moreover, in UG proposers became less inclined to deliver food across sessions (-0.26 ± 0.11, $\chi^2=5.82$, df=1, p=0.016). Thus, in both games chimpanzee proposers paid attention to the cost. They seemed to pay attention to the gift for the partner particularly in UG, although they decreased the food delivery over sessions.

Ultimatum game: acceptance rates

Recipients accepted all offers above zero whereas zero offers were accepted in 58.3 ± 7.1% of trials. GLMM04 was not significant compared to the null-model ($\chi^2=8.09$, df=5, p=0.151), neither was a reduced without the interaction ($\chi^2=6.89$, df=4, p=0.142).

Reciprocity

Except for a male-male dyad in which one subject reciprocated prosocial offers (see Tables S9, S10 and Figure S2), we found no evidence for short-term reciprocity: neither the offers in the previous trial (GLMM05) nor the average offers in the previous session (GLMM06) had a significant effect on performance.

Communication

All recipients except one sometimes pointed to a preferred option in the social games (13.4 ± 5.2 % of all trials, range: 0 – 42.7%). Recipients pointed usually before the proposers had chosen (98.0 ± 1.7 % of pointing trials). We found no evidence for a significant difference in pointing frequencies between the UG (mean ± SE: 22.0 ± 7.8%) and DG (8.6 ± 4.4%; see Table S13 and GLMM07 in the SI). We found no evidence that pointing changed the likelihood of the proposers providing food for the recipients (GLMM08, see Table S14). Direct interactions between participants occurred only 34 times (5.9% of all trials). Twenty-nine of these interactions occurred in the UG and five in DG. Due to the small number of instances, we could not analyze whether there was a significant effect of these interactions on the proposer's performance.

DISCUSSION

We tested chimpanzees using an iterated UG/DG protocol. Unlike humans, chimpanzee responders behaved as rational maximizers, invariably accepting offers larger than zero, something that is inconsistent with advantageous or disadvantageous inequity aversion, at least in the context of bargaining games and bearing in mind that our study does not cover all the aspects typically addressed in studies with adult humans. This is a very strong finding that has now been replicated in three other studies (Jensen et al., 2007; Kaiser et al., 2012; Proctor et al., 2013). Similarly to Jensen and colleagues' study (2007), chimpanzees accepted more than half of the zero offers. It has been argued that such high acceptance rates might indicate poor understanding of the task (Brosnan, 2013). However, we have provided robust and stable evidence of subjects' understanding of the contingencies of the game, which required paying attention to 1) the quantities on their side, 2) the opposite side, and 3) the consequences of choosing between the two options available. Another explanation for the lack of rational maximization is that long delays to reject may increase "false" acceptances to make a new trial start (Smith & Silberberg, 2010). However, this explanation is unlikely since we reduced the rejection period to 15 seconds (lower than 60s in Jensen et al., 2007 and 30s in Proctor et al., 2013) and kept the time between trials constant. Thus, as Henrich and Silk argued (2013), in a game where both accepting and rejecting a zero option invariably leads to a zero outcome, rejections may occur at chance (in accordance with our results) and still be compatible with rational maximization.

Proposers provided more food to conspecifics in the DG than when they played alone. In fact, such prosocial offers resemble those made by humans in the same game and are also in line with the change of preferences to offer more in social rather than non-social conditions of Proctor and colleagues's study (2013). However, proposers offered the same in the UG regardless of the presence of the partner, which differs from Proctor et al.'s (2013), where proposers offered more than expected in an UG. Such finding is puzzling from the point of view of classical economics. Brosnan & de Waal (2014) suggested that prosociality or anticipatory avoidance of conflict could explain this result. However, some methodological concerns made these explanations contentious. The absence of rejections might be due to the presence of a begging experimenter as well as to the fact that "neither species was explicitly trained that refusal was an option" (Proctor et al., 2013).

We found some evidence of a calculated prosociality that regulates gifts provided the proposers prefer not incurring costs. Probably the proposer first and foremost focused on her own payoffs, and secondarily, on her partner's. Interestingly, proposers did not offer more in the UG than the DG, as would have been expected for the sake of avoiding rejections. Perhaps the recipients' behavior can explain this outcome. While human proposers face high risk of rejection, chimpanzee proposers do not, given the high acceptance rate of their conspecifics. Responders accepting half of the time do not force proposers to be generous, since any selfish offer is likely to be accepted at least half of the time. This would justify the significant decrement of prosocial offers in UG, but it would not explain doing so also at no cost. One explanation might be that proposers facing a rejection of a selfish option would not be willing to reward the partner with food in a future trial and persist in offering less and less food. This would be similar to continue punishing the recipient for rejecting instead of rewarding the recipient to make him more willing to accept. If that was the case, there would be no signs of second-order inequity aversion in chimpanzee proposers after the recipients' refusals, contrary to previous interpretations (Brosnan & de Waal, 2014), but a lack of strategic behavior characteristic of human proposers' performance.

Despite large methodological differences, the four studies conducted so far (Jensen et al., 2007; Kaiser et al., 2012; Proctor et al., 2013 and the present one) have consistently shown that chimpanzees seem to differ when they play UG and DG, suggesting a divergent evolutionary pathway in the consideration of fairness. It is especially remarkable that no ape had rejected any offer different from zero so far. Kaiser and colleagues (Kaiser et al., 2012) argued that chimpanzee recipients in these games may not interpret a low offer as unfair. Although chimpanzees share food routinely, they did not usually offer food to each other (Gilby, 2006), so perhaps any offer is surprising and thus no unfairness is perceived. In contrast to humans, where the majority of cultures impose some kind of justice that is likely to be claimed and to cause rejections if not accomplished, non-human primates do not seem to possess an agreement on how to split windfall resources. Hence, rejections are probably only present in societies which define themselves as a community with some agreement on abstract entitlements among its members (which may explain why humans are more likely to reject a low offer from another human but not from a computer (Blount, 1995)). One could argue that we would have obtained different results if we had used much more valuable or much larger rewards. However, due to their natural occurrence, we would argue that smaller rather than very large windfalls are likely to be more common on a daily basis, and consequently, more relevant.

The virtual absence of rejections in the UG has also to be squared off with the seemingly contradictory results from other studies with non-human primates. For instance, a task that required the same effort from pairs of individuals but rewarded them differentially fostered rejection in capuchin monkeys (Brosnan & de Waal, 2003 but see also Bräuer, Call, & Tomasello, 2009; Silberberg, Crescimbene, Addessi, Anderson, & Visalberghi, 2009). Why did capuchin monkeys reject food in that study and chimpanzees did not when playing the UG? Windfall resources are not common in nature but effortful activities (e.g. hunting, foraging) are. Thus, non-human primates may consider merit rather than equality as a measuring rod for fairness, making deservingness comparable to something factual rather than to something abstract. Therefore, in order to obtain a deeper understanding of non-human primates' concept of fairness and force proposers to face the risk of a potential rejection, novel tasks with factual comparisons, such as different labour investments, are required.

Communication and establishing turn taking is one way by which human children manage to split windfalls equally in coordination games (Grüneisen, 2015; Sánchez-Amaro, Duguid, Call, & Tomasello, 2016). We found no evidence that communication or reciprocity fostered a more equitable distribution of payoffs, in accordance to previous findings (Vonk et al., 2008). However, it is interesting to note that in our study only recipients (except for one single occasion) emitted pointing gestures to their proposer partners because pointing is usually reported between human experimenters and captive non-human primates (up to 71% of captive chimpanzees pointed to unreachable food in Leaven's studies (Leavens, Hopkins, & Bard, 2005)) rather than between conspecifics (Itakura, 1996).

In our case, pointing did not significantly alter the proposers' subsequent actions, but it seems clear that chimpanzee responders were trying to use some way of local enhancement that was inefficiently understood by proposers, as was previously reported in a similar proposer/recipient design (Silk et al., 2005). It is unlikely that chimpanzee responders in our study were trying to reach the food, because they did not point when the proposer was absent. Therefore, it seems that even when chimpanzees individually use pointing as a referential gesture to humans, they find difficulties to transfer the same meaning within their species, as if response to pointing was very limited between species. It might happen that proposers do not perceive themselves as the addressee of such communication (however, see orangutans' performance on referential pointing plus a discussion about the inferences required to comprehend pointing, Moore, Call, & Tomasello, 2015).

CONCLUSIONS

In conclusion, our results are compatible with the existence of intrinsic (although non-costly) prosociality and rational maximization behavior, but provide no evidence of inequity aversion. There were no signs of reciprocity and proposers did not change their behavior even if it led to rejection (contrary to the strategic behavior characteristic of human proposers' performance). These findings suggest that prosociality, inequity aversion and strategic behavior might have followed different evolutionary pathways in the two species.

AUTHOR CONTRIBUTIONS

Conceived and designed the experiments: NBG, JC, AD, MC. Performed the experiments: NBG, AD. Analyzed the data: CV, JC, NBG. Interpretation of data and writing of the paper: JC, NBG, CV.

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FIGURE LEGENDS

Figure 1. Illustration of the apparatus for the DG (a) and UG (b) in the condition 6/0 (background) 6/3 (foreground). The proposer is depicted on the left and the recipient on the right. In the DG, the recipient cannot reject the offer. In the UG, the recipient can respond to the offer by pulling the U-shaped rope (accept) or not (reject) once the proposer has chosen one option.

Table 1. Conditions and maximizing choices. Quantities used in non-social (Door Open/Door Closed) and social games. Depicted are the outcomes in each non-social condition based on a maximizing outcome. We also provide the labels of each pair of options used in social games to better illustrate the factors assessed (cost for the proposer; gift for the recipient)

Table 2. Summary of the main GLMMs performed. See more information in SI.

Figure 2. Proportion of trials (mean ± SE) of the common conditions in the Door open/closed non-social tests in which chimpanzees preferred the option that delivered food to the opposite side (over the default 6/0 option) as a function of cost and door state. * denotes significant deviations from the hypothetical chance level (dashed line), $p<0.05$, Wilcoxon signed-rank tests.

Figure 3. Proportion of trials (mean ± SE) in which chimpanzees preferred the option that delivered food to their partner's side over the default 6/0 option as a function of game (DG, UG), size of the gift for the partner (x/9 vs. x/3), and cost at the subject's side (cost: 5/x; no cost: 6/x). * denotes significant deviations from the hypothetical chance level (dashed line), $p<0.05$, Wilcoxon signed-rank tests.

Figure 4. Proportion of trials (mean ± SE) in which proposers selected the option that delivered food to their partner's side as a function of game (non-social control, DG, UG) and cost for the proposer. *denotes significant deviations from the hypothetical chance level (dashed line), $p<0.05$, Wilcoxon signed-rank tests.